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Pragian (Lower Devonian) stromatoporoids and rugose corals from Zújar (Sierra Morena, southern Spain)

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ABSTRACT. The locality Zújar at the boundary between the Badajoz and Córdoba provinces belongs to the Obejo-Valsequillo-Puebla de la Reina Domain. Within the fossiliferous reefal carbonates of Pragian age cropping out in Zújar, 10 stromatoporoid species and 7 rugose coral species are identified. The new rugose coral species *Martinophyllum miriamae* n. sp. is described. *Hexagonaria soraufi* Rodríguez García, 1978 is a subspecies of *Martinophyllum ornatum* Jell & Pedder, 1969. The Pragian fauna of Zújar is a typical fauna of the Old World Realm with remarkably close relationships to Arctic Canada and Australia. Most species have been recorded for the first time from Spain. No significant relationships to the Eastern Americas Realm are visible. Remarkable is, that none of the stromatoporoid species of Zújar is known from the famous Pragian reef complex of Koněprusy in Bohemia, meanwhile the rugose coral fauna (e. g. *Joachimastraea barrandei* Galle, Hladil & May, 1999) shows some relations. Some of the species found are ancestors of important constructors of the Middle Devonian reef complexes, demonstrating that the roots of the Givetian-Frasnian reef complexes reach down to the Pragian.

KEYWORDS: Biogeography, reef, Anthozoa, Porifera, Devonian, Spain, Obejo-Valsequillo-Puebla de la Reina Domain, new species.

1. Introduction

Within the Middle Devonian and Lower Upper Devonian, reefs and biostromes made by stromatoporoids and corals are common world-wide (Burchette, 1981; Fagerstrom, 1987; Kiessling et al., 2003). Consequently, Middle and Upper Devonian stromatoporoids and corals are well investigated. Going down the Devonian timescale, the frequency of reefs and the knowledge on its constructors decrease, provoking several questions. (As a help for readers which are not familiar with the Devonian: the Lower Devonian is subdivided from lower to upper into Lochkovian, Pragian and Emsian.)
One obvious question is, how deep the roots of the Middle to Upper Devonian reef complexes reach: Is the fauna of corals and stromatoporoids in the Lower Devonian (e.g. Pragian) reefs completely different, or do we find the first ancestors of the constructors of the Middle to Upper Devonian reefs?

Other questions concern the biogeography: During the Pragian and Emsian, provincialism of the shallow marine benthos reached its maximum (Boucot, 1988: 211-212; Oliver & Pedder, 1994: 185; May, 1996, 1997). Up to now, concerning the biogeographic relations of the Southern Spanish Lower Devonian, only some data on Emsian stromatoporoids exist (May, 2006, 2007). The relations of the Pragian coral and stromatoporoid fauna were not known.

Another related topic involves the stromatoporoids of the Eastern Americas Realm: The Lochkovian and Emsian in the Eastern Americas Realm contain a distinct stromatoporoid fauna, characterized by the occurrence of *Habrostroma*. However, in the Eastern Americas Realm, there are virtually no stromatoporoids known from the Pragian (for details see Stock, 1997a; Stearn, 2001). Consequently, Stock (1994: 26) assumed that the Eastern Americas stromatoporoids survived in an unknown refuge in Bohemia, France, or Spain. Consequently, we try to answer in this paper the question: "Took the stromatoporoids of the Eastern Americas Realm during the Pragian refuge in the Sierra Morena?"

2. Investigated material

A first investigation of the Lower Devonian rugose corals in the Sierra Morena (Badajoz and Córdoba provinces, Southern Spain) was made by Rodríguez García (1978). Based on this study, since 2003 a group of palaeontologists from the universities of Valencia, León and Madrid is studying the main outcrops of Devonian reefal carbonates in the Sierra Morena (Research Projects BTE2003-2065 and GR-UCM/910231). All these localities belong to the Obejo-Valsequillo-Puebla de la Reina Domain.

First, we studied the locality Guadámez-2 (with Emsian reefal carbonates) in the Badajoz province and the locality Peñón Cortado in the Córdoba province (May, 2006, 2007; Valenzuela-Ríos et al., 2006; Rodríguez et al., 2010; see Fig. 1 and 2). Based on the stromatoporoid fauna, May (2006: 35) assumed an Emsian age for the reefal carbonates of the locality Peñón Cortado, which contain much *Hexagonaria soraufi* Rodríguez García, 1978. However, later investigations based on conodonts revealed a Pragian age for these reefal carbonates (Valenzuela-Ríos et al., 2006).

Later we extended our study to the locality Zújar at the boundary between the Badajoz and Córdoba provinces (38º29'30''N, 1º46'W). The locality Zújar is about 13.5 km north-easterly of Valsequillo, within the valley of the river Zújar (Fig. 2). Outcropping are siliciclastic sediments and limestones of Lochkovian, Pragian and Famennian age. Brachiopods and conodonts prove that the limestones with corals and stromatoporoids are Pragian in age (Pardo Alonso & Valenzuela-Ríos, 2006; Valenzuela-Ríos et al., 2006).

The Pragian limestones of Zújar are a 60-70 m thick sequence, which starts with about 10-15 m platy limestones, which may contain many brachiopods (Pardo Alonso & Valenzuela-

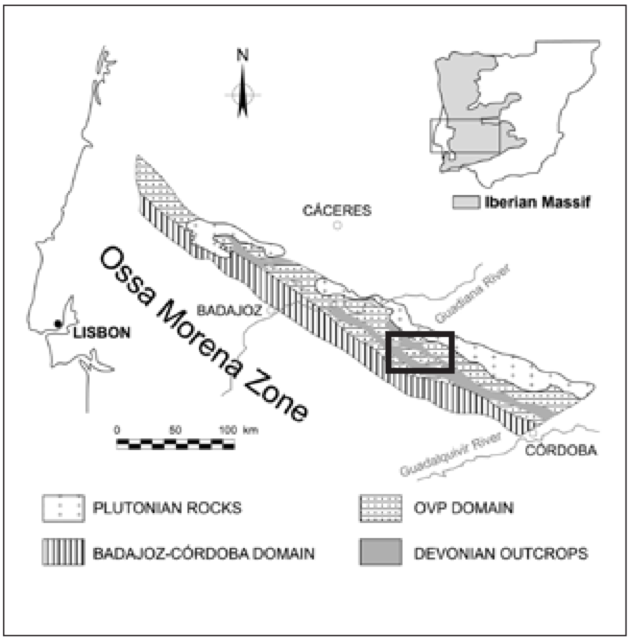

Figure 1. Structural map of the Ossa Morena Zone, showing the study area.

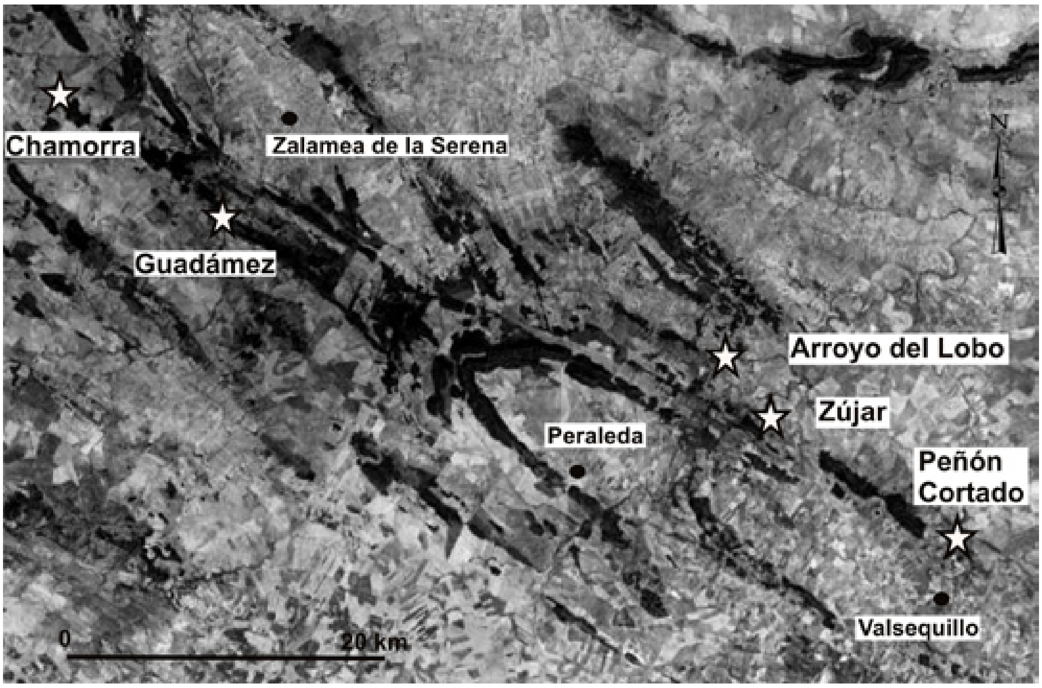

Figure 2. Location of studied outcrops. White asterisks mark the positions of the studied outcrops, meanwhile black dots mark the exact positions of three villages.

Ríos, 2006). In continuation follow about 17-32 m crinoidal limestones. Finally follow about 20-36 m bedded limestones with tabulate corals, stromatoporoids and rugose corals, which provided the fossils presented in this paper.

Furthermore we consulted material from other localities in the Sierra Morena (La Chamorra, Arroyo del Lobo, Peñón Cortado; see Fig. 2), especially the rugose corals described by Rodríguez García (1978) from the Pragian limestones of the locality Peñón Cortado. Further information on these localities is given by Rodríguez García (1978: 331-335) and May (2006: 31-32).

3. Systematic palaeontology

Up to now, in the Pragian limestones from Zújar, 10 stromatoporoid species and 7 rugose coral species have been identified.

Longitudinal and tangential (= transverse) thin sections have been taken from the stromatoporoid and rugose coral specimens collected. The methodology, terminology, and classification (including the genus definitions) follow those of Stearn (1993a), Stearn et al. (1999) and Hill (1981). The material is stored in the Departamento de Paleontología, Universidad Complutense, Madrid, under the numbers DPM-00276/Z1 to DPM-00276/ZE18.

3.1. Stromatoporoids

Nexililamina dipcreekensis **Mallett, 1971**
(Plate 1 A-B)

Material. From Zújar: DPM-00276/Z4, Z13, Z18.

Description and discussion. Within the vertical sections, the commonly superposed pillars are spool-shaped or Y- or V-shaped. Their frequency is mostly 11-12 (min. 9, max. 15) pillars/2 mm. There are 9-11 laminae /2 mm. Horizontal dissepiments between the laminae are common. These horizontal dissepiments are more or less parallel to the laminae and connect neighbouring pillars.

The colonies fit well with the redescription of *Nexililamina dipcreekensis* Mallett, 1971 by Webby & Zhen (1997: 35-36, fig. 12 C-F). The only visible difference is, that the vertical sections of the Spanish material show slightly more pillars than the type material (mostly 9-11 pillars/2 mm). Up to now, *Nexililamina dipcreekensis* has only been found in the Emsian-Eifelian of Queensland (Webby & Zhen, 1997).

Plectostroma altum **(Ripper, 1933)**
Plate 1 C-D

Material. From Zújar: DPM-00276/Z1, Z4, Z8, Z11, Z14, Z20, ZE9.
Description and discussion. The colonies fit well with the redescription of *Plectostroma altum* (Ripper, 1933) by Webby et al. (1993: 126-128, figs 7E-8D). Within the vertical sections, the density of pillars vary from 7-9 pillars/2 mm to 9-12 pillars/2 mm. The pillars have 0.03-0.06 mm thickness. There are 10-20 horizontal elements over a distance of 2 mm.

The type material of *Plectostroma altum* (Ripper, 1933) as well as the colonies from Zújar can be distinguished from *Plectostroma yunnanense* (Mansuy, 1914) and *Plectostroma salairicum* (Javorskij, 1930) by their shorter pillars and their more pronounced latilaminae (May, 2005: 152-154; Javorskij, 1930: 480, pl. 2; Prosh & Stearn, 1996: 15-16, pl. 1 figs 4-5). Furthermore, *Plectostroma salairicum* has a slightly higher density of pillars: 5-6 pillars/1 mm (Javorskij, 1930) or 6-8 pillars/1 mm (Prosh & Stearn, 1996).

Probably, the material from the Pragian limestones of Peñon Cortado, which May (2006: 32-34, fig. 3b; 2007: 142-143) assigned to *Plectostroma salairicum*, belongs to *Plectostroma altum*, too. *Plectostroma altum* was known up to now only from the Pragian of Victoria, Australia (Webby et al., 1993).

Stictostroma gorriense **Stearn, 1995**
(Plate 1 E-F)

Material. From Zújar: DPM-00276/Z23.

Description and discussion. The colony fits well with the description of *Stictostroma gorriense* Stearn, 1995 by Stearn (1995: 26, figs 1-2) and Prosh & Stearn (1996: 24-25, pl. 8 figs1-5). Within the vertical sections, the density of skeletal elements is: 9-11 pillars/2 mm and 11-13 laminae /2 mm. *Stictostroma gorriense* occurs within the Lower and Upper Emsian of Arctic Canada and Ontario (Stearn, 1995; Prosh & Stearn, 1996).

Stictostroma nunavutense **Prosh & Stearn, 1996**
(Plate 1 G-H)

Material. From Zújar: DPM-00276/ZE18.

Description and discussion. The colony fits well with the description of *Stictostroma nunavutense* Prosh & Stearn, 1996 by Prosh & Stearn (1996: 25-26, pl. 9 figs1-5). Within the vertical sections, the density of skeletal elements is: 4-6 pillars/2 mm and 7-8 laminae /2 mm. *Stictostroma nunavutense* was known up to now only from the Lower Emsian of Arctic Canada (Prosh & Stearn, 1996).

***Stromatopora* ex gr. *rarissima* Počta, 1894 - *polaris* (Stearn, 1983)**

Material. From Zújar: DPM-00276/Z8.

Description and discussion. This undoubted representative of *Stromatopora* is not very well preserved. It is very similar to the holotype of *Stromatopora rarissima* Počta, 1894 (see May, 2005: 194, pl. 40 fig. 2) and the described material of *Stromatopora polaris* (Stearn, 1983) (Stearn, 1983: 551–552, fig. 5; Stearn, 1990: 507, fig. 3.8; Prosh & Stearn, 1996: 31, pl. 14 fig. 5). *Stromatopora rarissima* and *Stromatopora polaris* are so similar, that they are possibly conspecific. May (2005: 194) was not able to define significative differences between them.

Stromatopora rarissima originates from the Wenlockian of Bohemia (May, 2005), meanwhile *Stromatopora polaris* occurs in the Upper Lochkovian to Upper Emsian of Arctic Canada (Stearn, 1983, 1990; Prosh & Stearn, 1996; Stearn, 2001: 14-15). Furthermore, similar forms are known from the Lower Emsian of Victoria (Webby et al., 1993:158–161, figs 5, 23, 24) and the Emsian of the Sierra Morena (May, 2006).

***Pseudotrupetostroma* cf. *pellucida* (Javorskij, 1955)**
(Plate 1 I-J)

Material. From Zújar: DPM-00276/Z3.

Description and discussion. The colony is not very well preserved. Nevertheless, it can be assigned to *Pseudotrupetostroma* Chalfina & Javorskij, 1971 because of its microstructure and its pillars, which are in many cases superposed over 2 to 4 interlaminar spaces. Within the vertical sections, the density of skeletal elements is: 6-9 pillars/2 mm and 7-8 laminae /2 mm. It can be distinguished easily from the only known Spanish *Pseudotrupetostroma* species, *P. anacontentoae* May, 2007. In *P. anacontentoae* May, 2007, the distances between the skeletal elements are much smaller. Furthermore, in the colony from Zújar, the astrorhizal canals are bigger, less frequent and and not oriented in the specific pattern of *P. anacontentoae* May, 2007 (May, 2007: 144-147, fig. 2).

Comparable to the colony from Zújar are two taxa: *Stromatopora pellucida artyschensis* Javorskij, 1955 and *Stromatopora pellucida pellucida* Javorskij, 1955. *Stromatopora pellucida artyschensis* Javorskij, 1955 from the Givetian of Siberia, the type species of *Pseudotrupetostroma*, has about 2 laminae per 1 mm (maximum 4 laminae per 1 mm) (Javorskij, 1955: 100–101). In *Stromatopora pellucida pellucida* Javorskij, 1955 from the Lower Devonian and the Givetian of Siberia, the laminae are spaced 8–9 per 2 mm and there are up to 6 pillars per 1 mm (Javorskij, 1955, p. 91–92).

The genus *Pseudotrupetostroma* Chalfina & Javorskij, 1971 is known from the Emsian to the Givetian in Australia, Asia, Canada, Spain and Central Europe (Stearn et al., 1999: 48; May, 2006, 2007; Salerno, 2008: 92-96). The material from the Pragian of Zújar is one of the oldest occurrences of the genus.

***Syringostromella zintchenkovi* (Chalfina, 1960)**
(Plate 1 K-L)

Material. From Zújar: DPM-00276/ZE2, ZE11, ZE16.

Description and discussion. The colonies ZE2 and ZE11 fit well with the descriptions of *Syringostromella zintchenkovi* (Chalfina, 1960) by Chalfina (1960: 327–328, pl. D-3 fig. 1), Webby et al. (1993: 163, figs 23-24) and Prosh & Stearn (1996: 34, pl. 15 figs 1-3). Within the vertical sections, the density of skeletal elements are: 3.5-6 (mostly 4-5) pillars/2 mm and 4-5 horizontal elements (mostly microlaminae) /2 mm. The pillars are 0.15-0.3 mm (mostly ca. 0.2 mm) thick.

The colony ZE16 resembles *Syringostromella labyrinthea* Stearn, 1990, because it has 4.5-6 pillars / 2 mm, slightly better developed coenostromes and a slightly more irregular growth. However, these differences do not justify separating ZE16 from *S. zintchenkovi*, because *S. labyrinthea* has 5-7 pillars /2 mm (Stearn, 1990: 507, figs 5, 7, 8).

Hitherto *Syringostromella zintchenkovi* has been found in the Upper Lochkovian of Russia (Chalfina, 1960), the Pragian of Victoria (Australia) (Webby et al., 1993), the Lower Emsian of Arctic Canada (Prosh & Stearn, 1996) and the Pragian and Emsian of the Sierra Morena (May 2006, 2007).

***Coenostroma* aff. *pustulifera* (Winchell, 1867)**
(Plate 2 C-D)

Material. From: a) Zújar: DPM-00276/Z27, Z33, ZE4. b) Arroyo del Lobo: DPM-00276/A12.

Description and discussion. The colonies are typical representatives of *Coenostroma*. Within the vertical sections, the dimensions of skeletal elements are: 4 coenostromes /2 mm, coenostromes are 0.2-0.5 mm thick, 7-14 pillars / 2mm, pillars are 0.08-0.22 mm thick. Among all species assigned to *Coenostroma* by Stearn (1993b), the colonies fit best with the redescription of *Stromatopora pustulifera* Winchell, 1867 from the Middle Devonian of Michigan by Galloway & Ehlers (1960: 54-56, pl. 2). However, *pustulifera* has 6 coenostromes /2 mm (Galloway & Ehlers, 1960).

***Habrostroma centrotum* (Girty, 1895)**
(Plate 2 A-B)

Material. From Zújar: DPM-00276/Z10, Z18.

Description and discussion. The colonies fit well with the descriptions of *Habrostroma centrotum* (Girty, 1895) by Stock (1988: 14-15, figs 4-5; 1991: 905-906, fig. 5; 1997b: 545, figs 4.1-2) and Stock & Burry-Stock (2001). Within the vertical sections, there are 6-7 coenostromes /2 mm and 4-8 coenosteles /2 mm. The horizontal skeletal elements dominate over the vertical elements and cystlike microlaminae are rare. *Habrostroma consimile* (Girty, 1895) is very similar to *Habrostroma centrotum*, but has much more cystlike microlaminae (Stock & Burry-Stock, 2001).

Habrostroma centrotum (Girty, 1895) is known from the Lochkovian of New York and Arctic Canada (Stock, 1997b; Stock & Burry-Stock, 2001, 2007) and the Pragian of northern Spain (Fernández-Martínez et al., 2010: 314-316, figs11 E-F).

***Amphipora* sp.**
(Plate 2 E-F)

Material. From Zújar: DPM-00276/ZE13.

Description and discussion. The material consists of branches with 1.1-1.9 mm diameter without a clearly visible axial canal. The cosmopolitan *Amphipora ramosa* (Phillips, 1841) as well as *Amphipora porrecta* (Webby, Stearn & Zhen, 1993) from the Pragian of Victoria have thicker branches with a better developed axial canal (Stearn, 1997: 845-849, figs 1-11; Webby, Stearn & Zhen, 1993: 177-179, fig. 30).

3.2. Rugose corals

***Loyolophyllum (Fasciloyolopyllum) qinlingensis* (Cao in Cao et al., 1983)**
(Plate 3 I-J)

Material. From Zújar: DPM-00276/Z16.

Description and discussion. The material consists of corallites of *Loyolophyllum (Fasciloyolopyllum)* Zhen, 2007 which are grown together with stromatoporoids. Sections of juvenile stages of corallites have 1.8 mm diameter and 8 x 2 septa. Adult stages of corallites with 4.7 mm diameter have 14-15 x 2 septa and a peripheral stereozone of 0.7-1.0 mm thickness with rare dissepiments. The material fits well with the description of *Battersbyia qinlingensis* Cao in Cao et al., 1983 from the Early Devonian of northwest China (Cao et al., 1983: 137, pl. 46 figs 7a–b). *Loyolophyllum (Fasciloyolophyllum) parallelum* (Etheridge, 1899) from the late Eifelian to early Givetian of New South Wales has 2.2 mm in average corallite diameter and a smaller peripheral stereozone (Zhen, 2007: 204-206, figs 2-3).

Grypophyllum jenkinsi **(Strusz, 1966)**
(Plate 2 K-L)

Material. From Zújar: DPM-00276/ Z24, ZE18.

Description and discussion. Solitary coralla of *Grypophyllum* of 12-18 mm diameter with 56-62 septa and some lonsdaleoid dissepiments. Coralla without prominent rejuvenescence, septa not axially contorted. The material fits well with the descriptions of *Grypophyllum jenkinsi* (Strusz, 1966) by Strusz (1966: 562-563, pl. 87 figs 3-4) and Blake (2010: 90-92, fig. 55). Within the type material, usually the coralla have 15-20 mm diameter and 50-60 septa (Strusz, 1966: 562). The type material originates from the Garra Formation of New South Wales (Strusz, 1966) which is Lochkovian to Pragian in age (Trotter & Talent, 2005: 6). Blake (2010) found this species in the Givetian of Queensland.

Chostophyllum **ex gr. *gregorii* (Etheridge in Jack & Etheridge 1892)**
(Plate 3 M-N)

Material. From Zújar: DPM-00276/Z18.

Description and discussion. Solitary corallum of 17 mm diameter with 62 peripherally dilated septa, which resembles several Givetian to Frasnian species assigned to the genera *Temnophyllum* Walther, 1929, *Pseudozaphrentis* Sun, 1958 and *Chostophyllum* Pedder, 1982 (for discussion of the genera see McLean, 1993a). The closest similarity exists with *Chostophyllum gregorii* (Etheridge in Jack & Etheridge 1892) from the Givetian of Queensland (Zhen & Jell 1996: 82-83, pl. 13 figs 7-10). Material which is conspecific or at least very similar to *Chostophyllum gregorii* is described by Blake (2010: 121-122, fig. 86) from the Emsian or Eifelian of Queensland and by Strusz (1965: 537, pl. 73 figs 4-5) from the Lochkovian to Pragian Garra Formation of New South Wales (Trotter & Talent, 2005: 6).

Martinophyllum ornatum sorau fi **(Rodríguez García, 1978)**
(Plate 3 A-B, 3 E-F)

Material. From: a) Zújar: DPM-00276/Z27, Z31, Z34. b) Pragian of Peñon Cortado: V24/7 (=holotype; Pl. 3 E-F), DPM-00276/P8. c) Arroyo del Lobo: DPM-00276/A18. d) La Chamorra: DPM-00276/C24.

Description and discussion. The cerioid coralla are typical representatives of *Martinophyllum* Jell & Pedder, 1969. Within the material from Zújar, the adult corallites have 3.6-4.8 mm diameter and 26-28 (sometimes up to 30) septa. They fit very well with the holotype of *Hexagonaria soraufi* Rodríguez García, 1978 from the Pragian limestones of the locality Peñón Cortado and the original description of this species by Rodríguez García (1978: 340-342, pl. 1 figs 7-9). They are very similar to *Martinophyllum ornatum* Jell & Pedder, 1969, the type species of *Martinophyllum*, which has slightly larger corallites, slightly more septa and a slightly broader dissepimentarium (Jell & Pedder, 1969: 736-737, pl. 95 figs 4, 6, 8) and is known in Queensland from beds of upper Lochkovian or lower Pragian age (Webby & Zhen, 1997: 5).

It should be noted, that the septa of *soraufi* are not as clearly fusiform as in *ornatum*. However, as well as in *ornatum* specimens with strongly fusiform septa coexist with specimens with weakly fusiform septa (compare Jell & Pedder, 1969: pl. 95 figs 6, 8), in *soraufi* specimens with weakly fusiform septa coexist with specimens with cuneiform septa (compare Plate 3 A, E). These differences justify treating *soraufi* as a subspecies of *ornatum*. Probably, *Martinophyllum ornatum soraufi* (Rodríguez García, 1978) could be used as index fossil for Pragian. However, it should be noted that Sorauf (1969: 185-186, pl. 36 figs 1-5) described from the Emsian of western France as *Hexagonaria* sp. cf. *longiseptata* material which belongs to *Martinophyllum ornatum soraufi*.

Coen-Aubert (2002: 33, pl. 4 figs 3-4) compares *soraufi* with *Argutastrea? pradoana* (Haime in De Verneuil & Barrande, 1855). It is true, that the transverse section of *pradoana* shows some similarities with *soraufi*. However, in *pradoana* the corallites have 4.3-6.7 mm diameter and 30-34 septa. Furthermore, the longitudinal section of *pradoana* is much more *Argutastrea*-like with steeply inclined dissepiments and preferentially concave tabulae and tabellae (Coen-Aubert, 2002: 33, pl. 4 figs 3-4).

Martinophyllum miriamae **n. sp.**
(Plate 3 C-D, 3 G-H)

Derivation of name. The species is named in honour of Miriam May Contento, fourth daughter of Andreas May.

Type locality and horizon. Zújar, Pragian limestone.

Holotype. DPM-00276/ZE10, Pl. 3 C-D.

Paratype. DPM-00276/ZE6, Pl. 3 G-H.

Diagnosis. *Martinophyllum* species with 3.5-6.2 mm adult corallite diameter and more or less strongly reduced septa. Maximum are 32 septa.

Description. Cerioid corallum. In transverse section, adult stages have 3.5-6.2 mm (mostly 4.2-5.2 mm) corallite diameter and juvenile stages have 1.7-2.5 mm corallite diameter. If in adult stages the septa are more or less completely developed, 20-32 (mostly 28-30) septa are counted. Juvenile stages have up to 16 septa. As minimum 1-3 septa have been observed in juvenile as well as in adult stages. In transverse sections with very well developed septa, sometimes major and minor septa can be distinguished. In these cases, minor septa are somewhat shorter (about 65-80 percent of the length of the major septa) and may be slightly thinner. The major septa never reach completely to the centre, but always leave a central space of at least 1-2 mm diameter without any septa. In transverse sections with very well developed septa, all septa start at the outer wall, the septa are rarely interrupted and lonsdaleoid dissepiments do not occur. Frequently, the septa are slightly thickened within the peripheral part of the corallite. In transverse sections with very badly developed septa, only few, short, rudimentary septa are visible, which may start on lonsdaleoid dissepiments or on the outer wall. Between both extremes are continuous transitions.

The longitudinal section shows a clearly expressed periodicity between phases with well developed septa and badly developed septa. Within the phases with well developed septa, the longitudinal section resembles strongly *Martinophyllum ornatum ornatum* Jell & Pedder, 1969 and *Martinophyllum ornatum soraufi* (Rodríguez García, 1978), because the dissepimentarium is well developed, 0.4-1.2 mm broad and consists of 1-4 rows of globose to steeply inclined dissepiments, meanwhile the tabularium consists of densely spaced, arched tabulae and tabellae (14-17 horizontal elements per 5 mm distance). Within the phases with badly developed septa, the tabularium consists of widely spaced horizontal, inclined or arched tabulae and tabellae (4-6 horizontal elements per 5 mm distance) and the dissepimentarium is missing or consisting of remarkably larger dissepiments.

Discussion. At the first glimpse, someone might assign this peculiar species to *Carlinastraea* Merriam in Merriam, McKee & Huddle, 1976, *Utaratuia* Crickmay, 1960, or *Tawuphyllum* Pedder, 1980. However, each of these genera can be excluded easily: *Carlinastraea* Merriam in Merriam et al., 1976 has much thicker walls and completely different longitudinal sections (see Merriam et al., 1976: 32-34, pl. 6-7). *Utaratuia* Crickmay, 1960 can be easily distinguished by its longitudinal section as well as by the lack of transverse sections with well developed septa (see Jell & Hill 1970). Again, *Tawuphyllum* Pedder, 1980 can be easily distinguished by its longitudinal section. Furthermore, in *Tawuphyllum* the septa are well developed within the tabularium and suppressed within the dissepimentarium (see Pedder, 1980: 602-606, pl. 5), but in *Martinophyllum miriamae* n. sp. it is the contrary.

If there were only the phases with badly developed septa, no-one would assign this material to *Martinophyllum* Jell & Pedder, 1969. However, within the phases with well developed septa, the corallites strongly resemble *Martinophyllum ornatum ornatum* Jell & Pedder, 1969, the type species of *Martinophyllum*. In fact, corallite diameter and maximum number of septa are comparable to *Martinophyllum ornatum ornatum* Jell & Pedder, 1969 (p. 736-737, pl. 95 figs 4, 6, 8). Nevertheless, *Martinophyllum miriamae* n. sp. is distinguished from *Martinophyllum ornatum ornatum* and all other described species of *Martinophyllum* by the occurrence of corallites with strongly reduced septa. Furthermore, within *Martinophyllum ornatum ornatum* no such big central space without any septa exists. The other *Martinophyllum* species described by Jell & Pedder (1969) as well as *Martinophyllum daerdongense* Yu & Liao, 1982 from the Lower Devonian of Tibet (Yu & Liao, 1982: 106, pl. 2-3), *Martinophyllum altiaxis* Pedder, 1984 from the Lower Emsian of Canada (Pedder 1984: 320-322, figs 10-21) and *Martinophyllum planofundalis* Erina in Kim et al., 2007 from the Emsian of Uzbekistan (Kim et al., 2007: 193, pl. 55, figs 2-3) have larger corallites and more septa than *Martinophyllum miriamae* n. sp. *Martinophyllum ornatum soraufi* (Rodríguez García, 1978) has slightly smaller corallites and slightly less septa than *Martinophyllum miriamae* n. sp.

Important is the fact, that there are two coralla of *Martinophyllum miriamae* n. sp., which are distinguished from *Martinophyllum ornatum soraufi* (Rodríguez García, 1978) not only by their growth periodicity, but also by their skeletal dimensions. All coralla of *Martinophyllum ornatum soraufi* (Rodríguez García, 1978), which were found in Zújar, did not show any growth periodicity. From this observation it can be deduced, that the growth periodicity of *Martinophyllum miriamae* n. sp. was genetically induced. Nevertheless, we have not enough data to decide, if the growth periodicity was the response to extrinsic factors like sedimentation rate or length of the day or if it was an expression of intrinsic factors like periods of different intensity of reproduction.

Distribution. Not known outside the type locality.

***Joachimastraea barrandei* Galle, Hladil & May, 1999**
(Plate 2 H-J, 3 K-L)

Material. From Zújar: DPM-00276/Z35; from the Pragian of Peñon Cortado: PCR'-5, PCR-14; from La Chamorra: DPM-00276/C27.

Description and discussion. The well preserved material from Zújar has 4.0-5.5 mm corallite diameter and fits in all details (including the development of the dissepiments) very well with *Joachimastraea barrandei* Galle, Hladil & May, 1999, a genus and species which was known up to now only from the Pragian of Koněprusy (Bohemia) (Galle, Hladil & May, 1999: 182-184, pl. 1 figs 1-7, pl. 2 figs 1-5). The material from the Pragian limestones of Peñon Cortado and the material from La Chamorra are without any doubt conspecific.

***Rhizophyllum* ex gr. *bohemicum* Počta, 1902**
(Plate 3 O-P)

Material. From Zújar: DPM-00276/Z34.

Description and discussion. Coralla of *Rhizophyllum* with 13.2-17 mm diameter. Except of their much smaller size, the coralla are similar to *Rhizophyllum bohemicum* Počta, 1902 from the Pragian of Koněprusy (Bohemia) (Oliver & Galle, 1971: 84-85, pl. 2 fig 1-4, pl. 24 fig. 3).

4. Conclusions

4.1. Importance of the described fauna

That the described fauna is very important, is demonstrated by following comparison: Up to now, there were known from only three localities of Lower Devonian age of the Sierra Morena 11 stromatoporoid species (May, 2006, 2007) and 8 rugose coral species (Rodríguez García, 1978; concerning *Disphyllum pedrosense* Rodríguez García, 1978 see Rodríguez & Soto, 1979). In the Pragian limestones of Zújar, 10 stromatoporoid species and 7 rugose coral species were identified. This is almost as many as were known up to now in total from the Lower Devonian of the Sierra Morena.

Only one species from Zújar is completely new. However, most species collected in Zújar have been recorded for the first time from Spain. The exceptions are:

- 2 stromatoporoid species (*Stromatopora* ex gr. *rarissima – polaris*, *Syringostromella zintchenkovi*) and 1 rugose coral species (*Martinophyllum ornatum soraufi*) were known from other localities in the Sierra Morena.
- The stromatoporoid *Habrostroma centrotum* has recently been described from northern Spain (Fernández-Martínez et al., 2010).
- The stromatoporoid *Amphipora* is ubiquitous (May, 1993b; Stearn, 1997).

4.2. Biogeographic relations

The Pragian fauna of Zújar is a typical fauna of the Old World Realm with remarkably close relationships to Arctic Canada and Australia (New South Wales, Queensland, Victoria). No significant relationships to the Eastern Americas Realm are visible. *Habrostroma* is a characteristic stromatoporoid genus of the Eastern Americas Realm (Stock, 1990: 258; Stock, 1994; Stock, 1997a: 285; May, 2006: 36). However, *Habrostroma centrotum* is known to have immigrated into the Old World Realm (Stock & Burry-Stock, 2001, 2007; Fernández-Martínez et al., 2010). *Coenostroma pustulifera* is known from Michigan (Eastern Americas Realm) (Galloway & Ehlers, 1960), but the genus *Coenostroma* is widespread in the Old World Realm (Stearn et al., 1999: 53). Concluding, there is no hint, that the stromatoporoids of the Eastern Americas Realm during the Pragian took refuge in the Sierra Morena.

Remarkable is, that none of the stromatoporoid species of Zújar is known from the famous Pragian reef complex of Koněprusy (Bohemia) (compare May, 2005), meanwhile the rugose coral fauna shows similarities due to the occurrence of *Joachimastraea barrandei* Galle, Hladil & May, 1999 and *Rhizophyllum* ex gr. *bohemicum* Počta, 1902. Incidentally, these faunal relations between Koněprusy and Zújar are also demonstrated by the auloporid tabulate coral *Remesia koneprusiana* Galle, Hladil & May, 1999 (see Pl. 2G), which we found together with *Rhizophyllum* in DPM-00276/Z34.
Zújar has only *Habrostroma centrotum* in common with the Pragian fauna described by Fernández-Martínez et al. (2010) from Northern Spain.

4.3. Correlations with other localities in the Sierra Morena

The rugose corals described herein suggest a Pragian age for the limestones of the localities Arroyo del Lobo and La Chamorra (Fig. 2). For Arroyo del Lobo, no dating has been available up to now. Based on stromatoporoids, May (2006) suggested an Emsian age for La Chamorra. However, the dating based on rugose corals is more trustworthy.

4.4. Are there Pragian roots of the Middle Devonian reef complexes?

Among the stromatoporoid genera found in Zújar, the genera *Plectostroma*, *Stictostroma*, *Stromatopora*, *Pseudotrupetostroma*, *Habrostroma* and *Amphipora* are important constructors of the Middle Devonian reef complexes (e.g. Zukalová, 1971; Flügel, 1974; May, 1988, 1993b; Salerno, 2008). The rugose coral *Grypophyllum* is a characteristic member of the Middle Devonian reefs, too (e.g. Birenheide, 1978; Galle et al., 1988; May, 1993a; Wrzolek, 1993: 219; Schröder, 2005). In similar way, *Chostophyllum* is widespread in the Givetian and the closely related genus *Temnophyllum* is common in the Givetian to Frasnian reefs (Galle et al., 1988; McLean, 1993a; Wrzolek, 1993; Schröder, 2005).

From several places, especially in Australia, first occurrences of "typical" Givetian-Frasnian rugose coral genera and stromatoporoid genera are known from beds of Pragian or similar age (e.g. Strusz, 1965, 1966; Fedorowski & Gorianov, 1973: 29-30; McLean, 1993b: 58; Webby et al., 1993; Zhen, 1995; McLean, 2005: 29-30; May, 2005; Kim et al., 2007: 188). The same patterns can be shown also in tabulate corals. For example, *Scoliopora* is an important reef builder within the Givetian-Frasnian reef complexes (e.g. Galle et al., 1988; May, 1988: 184), but the oldest species of the genus are known from reefs of Pragian age (Hladil, 1989: 225-226; May & Pohler, 2009). Another example is *Syringopora praehanshanensis* May, 2005, the Pragian precursor of the Middle Devonian commensalic *Syringopora* species (for details see May, 2005: 221-226, 234-235).

Definitely, the roots of the Givetian-Frasnian reef complexes reach down to the Pragian.

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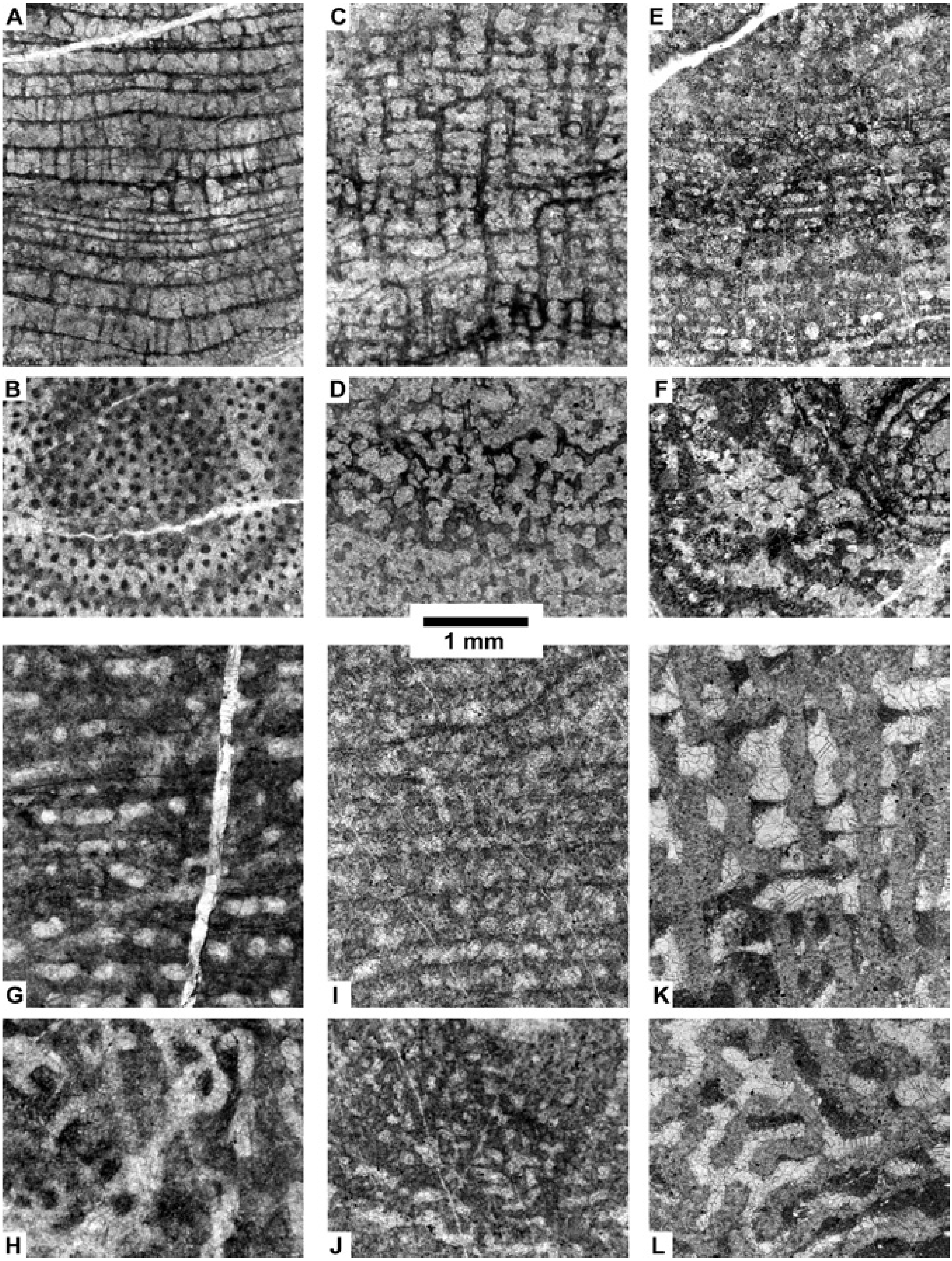

Plate 1. A-B: *Nexililamina dipcreekensis* Mallett, 1971, Pragian of Zújar, DPM-00276/Z18, (A) longitudinal section, (B) tangential section. C-D: *Plectostroma altum* (Ripper, 1933), Pragian of Zújar, DPM-00276/Z14, (C) longitudinal section, (D) tangential section. E-F: *Stictostroma gorriense* Stearn, 1995, Pragian of Zújar, DPM-00276/Z23, (E) longitudinal section, (F) tangential section. G-H: *Stictostroma nunavutense* Prosh & Stearn, 1996, Pragian of Zújar, DPM-00276/ZE18, (G) longitudinal section, (H) tangential section. I-J: *Pseudotrupetostroma* cf. *pellucida* (Javorskij, 1955), Pragian of Zújar, DPM-00276/Z3, (I) longitudinal section, (J) tangential section. K-L: *Syringostromella zintchenkovi* (Chalfina, 1960), Pragian of Zújar, DPM-00276/ZE11, (K) longitudinal section, (L) tangential section. Scale bar is 1 mm.

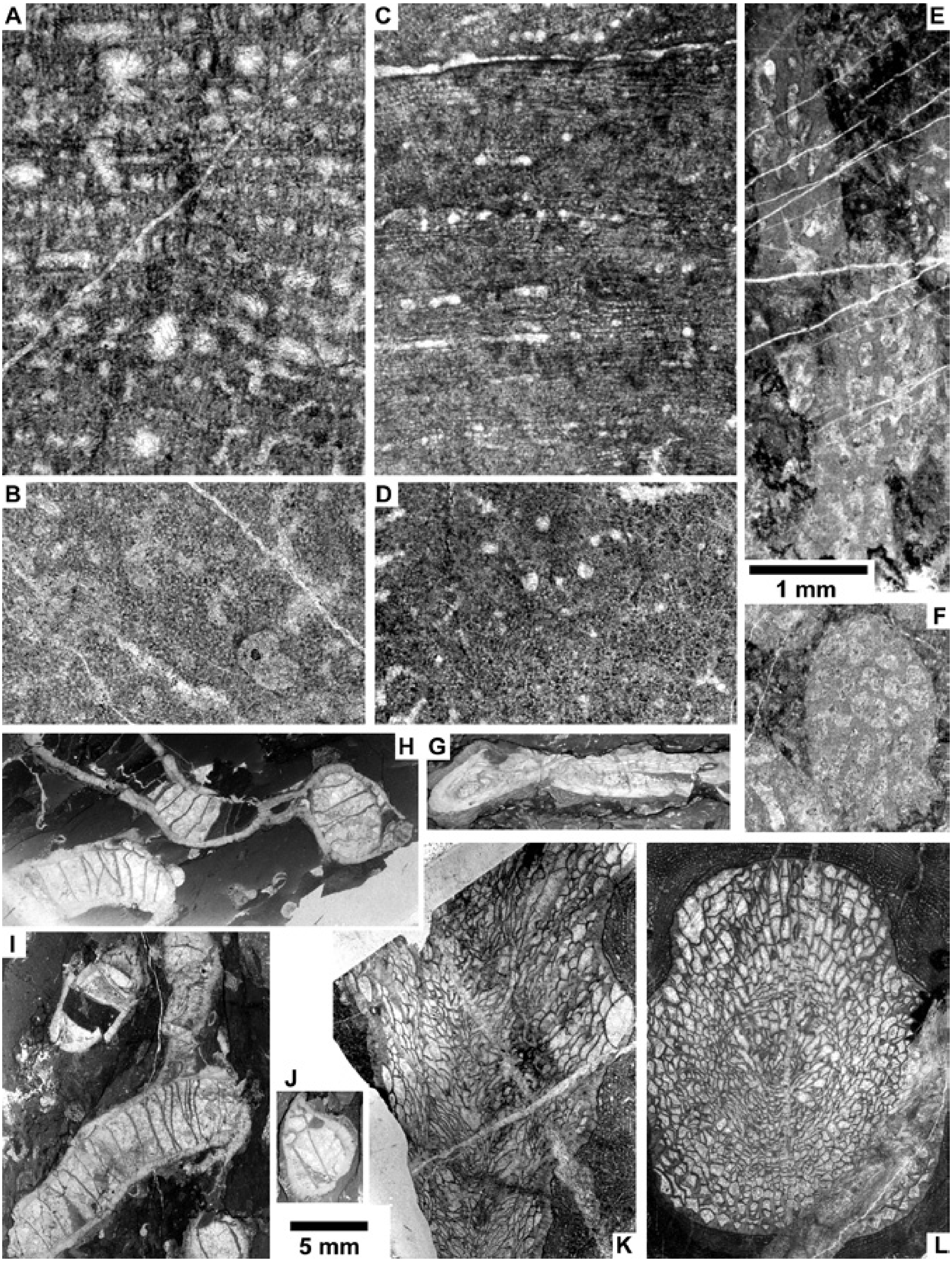

Plate 2. A-B: *Habrostroma centrotum* (Girty, 1895), Pragian of Zújar, DPM-00276/Z10, (A) longitudinal section, (B) tangential section. C-D: *Coenostroma* aff. *pustulifera* (Winchell, 1867), Pragian of Zújar, DPM-00276/Z33, (C) longitudinal section, (D) tangential section. E-F: *Amphipora* sp., Pragian of Zújar, DPM-00276/ZE13. G: Auloporid tabulate coral *Remesia koneprusiana* Galle, Hladil & May, 1999, Pragian of Zújar, longitudinal section, DPM-00276/Z34. H-J: *Joachimastraea barrandei* Galle, Hladil & May, 1999, Pragian of Zújar, DPM-00276/Z35, (H-I) longitudinal and transverse sections, (J) transverse section. K-L: *Grypophyllum jenkinsi* (Strusz, 1966), Pragian of Zújar, DPM-00276/Z24, (K) longitudinal section, (L) transverse section. Scale bar is 1 mm for A-F and 5 mm for G-L.

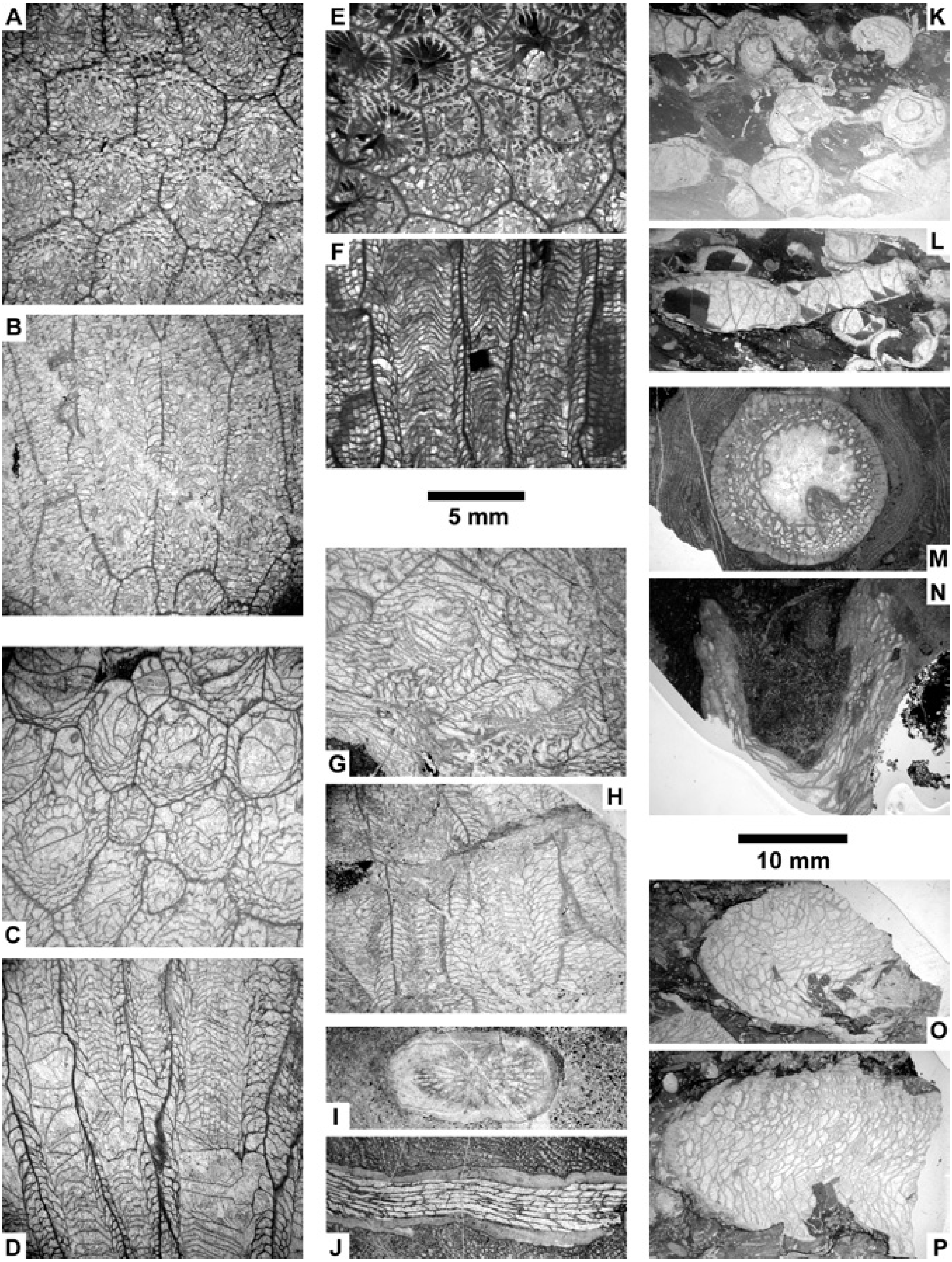

Plate 3. A-B: *Martinophyllum ornatum soraufi* (Rodríguez García, 1978), Pragian of Zújar, DPM-00276/Z31, (A) transverse section, (B) longitudinal section. C-D: *Martinophyllum miriamae* n. sp., holotype, Pragian of Zújar, DPM-00276/ZE10, (C) transverse section, (D) longitudinal section. E-F: *Martinophyllum ornatum soraufi* (Rodríguez García, 1978), holotype, Pragian of Peñon Cortado, V24/7, (E) transverse section, (F) longitudinal section. G-H: *Martinophyllum miriamae* n. sp., paratype, Pragian of Zújar, DPM-00276/ZE6, (G) transverse section, (H) longitudinal section. I-J: *Loyolophyllum (Fasciloyolopyllum) qinlingensis* (Cao in Cao et al., 1983), Pragian of Zújar, DPM-00276/Z16, (I) transverse section, (J) longitudinal section. K-L: *Joachimastraea barrandei* Galle, Hladil & May, 1999, Pragian of Peñon Cortado, PCR-14, (K) transverse sections, (L) longitudinal section. M-N: *Chostophyllum* ex gr. *gregorii* (Etheridge in Jack & Etheridge 1892), Pragian of Zújar, DPM-00276/Z18, (M) transverse section, (N) longitudinal section. O-P: *Rhizophyllum* ex gr. *bohemicum* Počta, 1902, Pragian of Zújar, DPM-00276/Z34, (O) transverse section, (P) longitudinal section. Scale bar is 5 mm for A-J and 10 mm for K-P.